Year End Report: Host plant choice in Fall Webworms (*Hyphantria cunea* Drury)

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Abstract: Fall webworms (*Hyphantria cunea* Drury) rank among the most generalist lepidopteran larvae and feed on hundreds of plants worldwide. However, they often exhibit local specialization; in Colorado, for instance, *H. cunea* are unequally distributed among about 20 woody host plants. The aim of my project is to explain the pattern of host tree choice in Colorado by quantifying the relative impacts of different selection pressures. First, *H. cunea* may prefer hosts that deliver the greatest nutritional benefit. To test this possibility, I am assessing bottom-up selection pressure by measuring pupal weight and larval feeding efficiency on local hosts. Another bottom-up selection pressure arises from the availability of hosts. Adult female *H. cunea* moths have limited time to deposit their eggs, and may prefer the most readily available trees. In order to test this possibility, I am establishing transects around utilized host trees to calculate the abundance of potential hosts. Finally, *H. cunea* could preferentially choose hosts that confer more safety from their natural enemies. I am measuring top-down selection pressure by recording the parasitism rate of fall webworm larvae on different host plants. The results of my research will help us to understand the mosaic of ecological processes behind insect specialization.

Introduction: Fall webworms (*Hyphantria cunea* Drury) are moths native to the US and Canada and invasive in Europe and Asia. Their gregarious larvae spin extensive webs for protection and thermoregulation, usually on the outer branches of deciduous trees. *H. cunea* are noted generalists, and have been recorded feeding on more than 100 tree species in the eastern United States. However, they often specialize regionally. In Colorado, I have observed them on 17 different tree species, with a marked preference hierarchy. ***My first hypothesis is that H. cunea preferentially feed on trees that are the most widely available in Colorado, but are still high quality food sources (H1). Alternatively, my second hypothesis is that H. cunea prefer trees that provide them protection from natural enemies like predators and parasitoids (H2)***.

Theoretical Background: Although there are many mechanisms that control the distribution of herbivores, bottom-up and top-down forces are among the most important. Bottom-up control of herbivores is evident in the complex secondary defensive compounds and physical obstacles plants have evolved to protect themselves from herbivory, and coevolved mechanisms herbivores have to bypass those obstacles (Ehrlich and Raven 1964, Fitzgerald 2008). Studies have also revealed the prominent role that natural enemies play in structuring herbivore populations (Hairston et al. 1960, Bernays and Graham 1988). Many papers examine the evolution of tritrophic interactions and the relative influence of bottom-up and top-down controls to various systems (Singer et al. 2004, Denno et al. 2003, Gripenberg and Roslin 2008, Moreau et al. 2006, Turchin et al. 2003). Both natural enemies and plant defenses are evolutionary selection pressures that may lead to herbivore specialization and speciation (Jaenike and Selander 1980). The fact that, unlike the world-wide and eastern US populations, Colorado *H. cunea* only use a handful of hosts makes it a fitting species to study the influence of top-down and bottom-up effects on host use.

Rationale and Methods for H1: In Colorado, *H. cunea* can completely defoliate trees during outbreaks (Swain 1936). However, *H. cunea* and their expansive webs are usually more unattractive than harmful (Wilkes 2007). *H. cunea* females preferentially lay their eggs along open edges (e.g. roads, streams), which makes webs easy to find after the larvae have hatched out of the eggs and built a web.

To assess the relative abundance of available host trees, I recorded 72 trees with *H. cunea* webs along Colorado's Front Range in 2010 and 80 trees in 2011. The relative abundance of tree species neighboring the preferred host trees will provide insight into the options that were available to female moths as they searched for a place to lay their eggs. To determine the abundance of neighboring trees, I measured two 15 m transects in opposite directions along the edge and recorded all deciduous trees greater than 1 cm in diameter at breast height. I collected a voucher specimen from each tree for later identification.

To determine whether *H. cunea* fitness varies among host plants, I collected 10 caterpillars per web from a subset of host trees and reared them in the lab on their natal host until pupation. To estimate *H. cunea* fitness on different hosts, I weighed the pupae before storing them at 4° C for the winter. In Lepidoptera, pupal weight is a significant predictor of lifetime fitness (Slansky and Scriber 1985). We were able to test that prediction for *H. cunea* this summer by counting the eggs laid by 43 female moths and regressing number of eggs against the mothers' pupa weights. Every 2.35 mg of additional pupa weight corresponded to an additional egg ($T=4.59$, df, 42, $P<0.0001$).

Within the lab, I mated *H. cunea* adults in my colony and performed feeding trials with their offspring. I used a split-brood design; from each of 10 female moths, I reared 10 larvae on 4 host plants (n= 400 larvae) in individual containers in temperature and photoperiod controlled growth chambers. The four hosts were two of the most commonly used hosts (narrowleaf cottonwood and choke cherry) and two less commonly used hosts (alder and crab apple).

To measure feeding efficiency, another measure of host plant quality, I recorded the dry weight of frass (larval excrement) for each individual at 20 days of age until pupation. Feeding efficiency can be estimated by dividing pupal weight by dried frass weight (Wilkes 2007). If feeding efficiency is greatest on the most commonly used host plants, the result will support the hypothesis that *H. cunea* preferentially feed on the most nutritious hosts.

Rationale and Methods for H2: Native to North America, *H. cunea* were accidentally introduced to Hungary and Japan in the 1940s and spread to other parts of Europe and Asia in the following decades (Tadić 1983, Yang and Wang 2008). In China, *H. cunea* feed on 175 host tree species, including cultivated crops, and are considered a pest of economic importance (Yang and Wei 2006). In accordance with the enemy-release hypothesis, which states that freedom from native, co-evolved enemies is largely responsible for the success of invasive pests (Liu and Stiling 2003), managers in Europe and Asia imported North American parasitoids known to kill *H. cunea* larvae into their countries as a method of biological control (Tadić 1983).

The natural enemies I studied are parasitoid flies and wasps. Parasitoids are parasites that kill their hosts and account for about half of fall webworm larval mortality (Tadić 1983). When I collected *H. cunea* from their webs, adult parasitoids had already laid their eggs inside them. As I reared *H. cunea* in the lab in individual containers, I collected the parasitoids after they emerged from their caterpillar hosts.

Activity in Boulder County Parks and Open Space: From July 21st through August 22nd of 2011, I collected 15 *H. cunea* caterpillars from Tinsley, 12 caterpillars from Ador, 12 caterpillars from Davies, and 12 caterpillars from Betasso Homestead. We spent an estimated 5 hours on Boulder County Parks and Open Space properties either collecting larvae or host plant branches for feeding in the lab.

Preliminary Results: Out of 500 trees recorded on all transects in 2010, 365 (73%) were one of the twelve observed hosts and 135 (27%) were non-host deciduous trees. 38.2% of recorded trees were the same species as the host on their particular transect. I am currently in the process of analyzing the tree abundance data from 2010 and 2011.

Pupal weights varied significantly by host tree in 2010 (F=4.3801, df=6, P= 0.0003; Fig.1). Only pupae fed on crab apple were significantly lighter. It will be important to factor in 2011 pupal weight data from larvae hatched in captivity, because time spent feeding versus hiding from predation can impact the pupal weight of wild caught caterpillars. I am still in the process of analyzing pupal weights for 2011.

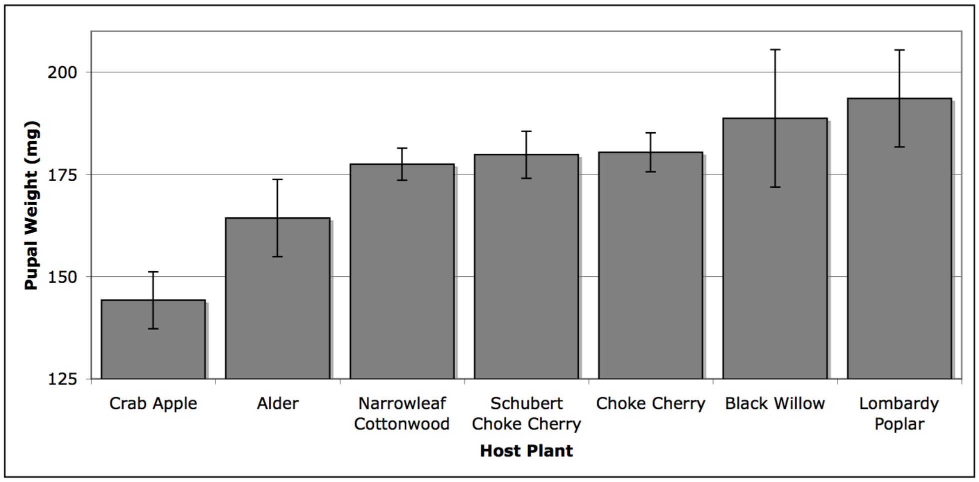

Figure 1. Average pupal weights of wild-caught *H. cunea* by host plant in 2010. Standard error bars are included.

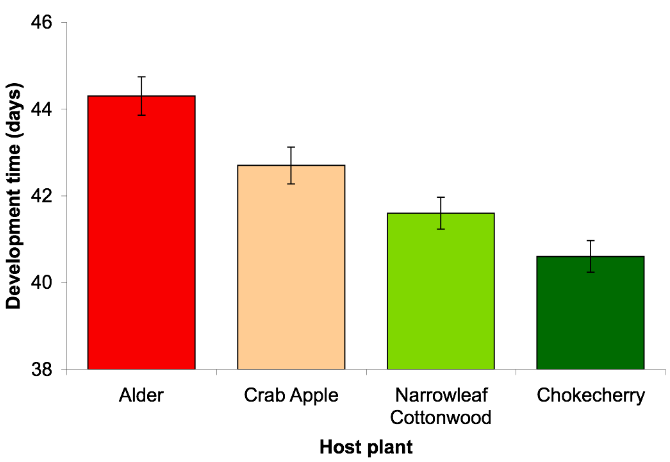

Figure 2. Development time from hatching to pupation on four host plants, 2011. Red represents the worst-case scenario for caterpillars and longest development time, while dark green is the best and shortest development time. Standard error bars are included.

Analysis of frass and pupal weights from 2011 is ongoing. However, the development time of H. cunea reared from eggs in 2011 conforms with pupal weight results from wild-collected larvae in 2010. Shorter development times from hatching to pupation can mean higher lifetime fitness because the larva had less exposure to predation. Development time was significantly different by host tree, and the host plants with the highest pupa weights, narrowleaf cottonwood and choke cherry, also had the shortest development times (F=14.795, df=3, P<0.0001; Fig. 2).

Parasitism rate in 2010 varied significantly by host plant (χ^2=15.384, df=4, P=0.004; Fig. 3). *H. cunea* larvae found on choke cherry and narrowleaf cottonwood had the highest parasitism rates, while larvae on alder and crab apple had the lowest at 5% each. I cannot fully analyze 2011 parasitism data until adult *H. cunea* and additional parasitoids emerge in the summer of 2012.

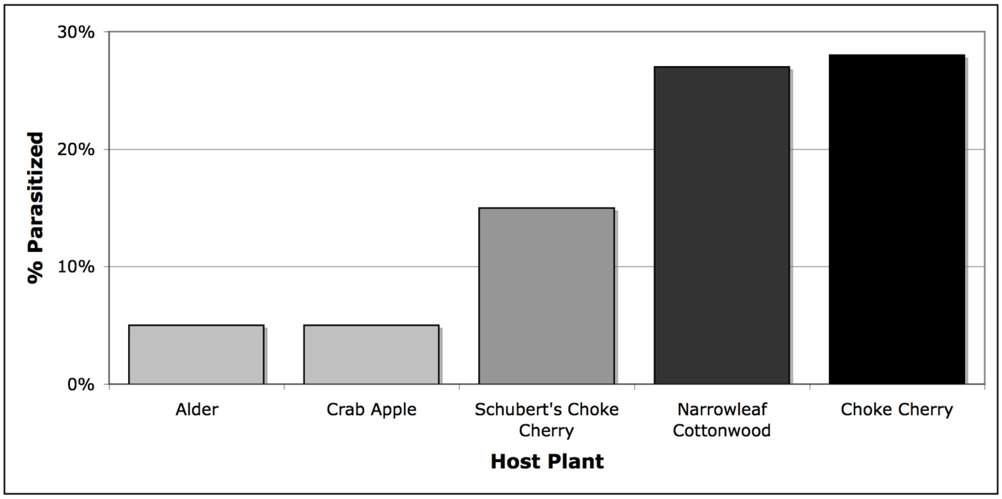

Figure 3. Parasitism rates of wild-caught H. cunea by host plant. The analysis excluded all host plants with fewer than 20 larvae. Dark colors represent higher parasitism rates.

Preliminary Conclusions and Future Directions: The preliminary analysis supports both plant quality and parasitism rate as driving factors for host selection by *H. cunea* on the Front Range. Host plants feeding the heaviest pupae, like narrowleaf cottonwood and choke cherry, were the most commonly used (abundance analysis ongoing), and had the shortest larval development times, but also had the highest parasitism rates. Host plants with lighter pupae, like alder and crab apple, also had lower parasitism rates. That apparent trade-off suggests that *H. cunea* select lower quality hosts to avoid natural enemies, but further research is necessary for confirmation.

I mentored five University of Denver undergraduate lab members on this project, and several have designed and partially executed their own *H. cunea* experiments. It is likely that one or several lab members will apply for a permit to continue research on *H. cunea* either next summer or the following year.

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